

Lifespan in male ants linked to mating syndrome

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Abstract Male ants have long been thought to leave the nest, swarm, mate and die in quick succession (*male aggregation syndrome*). However, the ancestors of the ants likely used *female calling*, where females advertise with pheromones for longer lived and presumably free living males. In this study, male lifespan was compared in four species from a Panama rain forest. Males of two species with aggregation syndrome (*Atta colombica* and *Azteca* sp.) lived only days after collection at a light trap, and their lifespan failed to increase when supplied sugar water ad libitum. In contrast, two species with female calling syndrome (*Ectatomma ruidum* and *Paraponera clavata*) lived up to 116 days when fed. These results link male lifespan to mating systems, and provide a framework to examine variation in how ant colonies invest in males.

Keywords Body size · Female calling syndrome · Life history · Male aggregation syndrome

Introduction

Although lifespan tends to increase with body size (Peters, 1983; Speakman, 2005), considerable size-independent variation can remain (Sibly and Brown, 2007). Some appears to be linked to tradeoffs between rates of survival and reproduction (Kozłowski and Weiner, 1997; Reznick, 1997; Dobson and Oli, 2007). An interesting variation of this problem involves sexual differences in lifespan: males

tend to increase fitness by increasing mating rate, while females tend to increase fitness by living longer (Trivers, 1972). Males are often the shorter-lived sex, engaging in riskier behaviours (Vollrath and Parker, 1992; Zuk and McKean, 1996), with diminished capacity for cellular maintenance (Cherif et al., 2003) and immune defence (Zuk and McKean, 1996; Rolff, 2002; May, 2007).

Ants (Hymenoptera: Formicidae) show an extreme version of this variation. Inseminated queens found colonies, and may live for decades (Keller and Genoud, 1997). Males, in contrast, do not take part in colony life (Bartz, 1982), have unique suites of traits (e.g. greatly reduced heads and mandibles, but often with eyes enlarged relative to females), and are thought to die shortly after mating (Boomsma et al., 2005). Compared to queens (e.g. Tschinkel, 1992; Keller and Passera, 1989; Johnson, 2002; Hahn et al., 2004), few studies have detailed what males do once they leave the natal colony (Baer, 2003; Heinze, 2004; but see Wiernasz et al., 2001; Baer and Boomsma, 2006; Mercier et al., 2007). One trait that may play a large role in determining male lifespan is the species' mating system.

Male and female alates find each other via two distinct syndromes. In the ancestral *female calling syndrome*, females attempt to attract males with pheromones, often near the natal site, and do not disperse until after mating (Hölldobler and Bartz, 1985; Boomsma et al., 2005). In *male aggregation syndrome*, male and female alates leave their natal nest at the same time, forming large male-dominated swarms (Boomsma et al., 2005) that for some species are characterized by competition among males for mating attempts (Hölldobler and Bartz, 1985). A key difference between these two syndromes from the male perspective is the availability of virgin females in time and space. In male aggregation, females are readily available

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and seek out males. In female calling, males have to search for matings that may be spread out over time. If true, males in the latter syndrome should be under selection to live longer than males that swarm.

To test this prediction, and a potential mechanism, male lifespan was monitored within four Neotropical ant species, two from each syndrome. Furthermore, half the males were provided with sugar water, and half with water only. Species that use female calling were predicted to feed outside the nest and thus live longer than those using male aggregation.

Materials and methods

From May to June 2007, male alates were captured in a lowland tropical forest on Barro Colorado Island (9°09'N, 79°51'W) in Panama. The species used in this study ranged widely in phylogeny and body size (Table 1). The two male aggregating species, *Atta colombica* and *Azteca* sp., form conspicuous swarms at discrete time intervals. In contrast to the aerial swarms of *A. colombica* (Weber, 1972; Baer and Boomsma, 2006) from which males were collected during the day, males of *Azteca* sp. (species-level identification of males was not possible) amassed in the evening, and were collected at lights at the forest edge (J. Shik, personal observation). Two female calling species (*Ectatomma ruidum* and *Paraponera clavata*) were also monitored. *E. ruidum* alates are found throughout the year (Kaspari et al., 2001), and females are thought to secrete a male attracting pheromone (Hölldobler and Haskins, 1977). Little is known about the mating system of *P. clavata*, but small numbers of alates were found continuously in flight traps from June to December (M. Kaspari, unpubl. data). During nights throughout the summer, males of both female calling species were observed at lights, where they were collected on the dates stated in Table 1.

Upon capture, males were placed in separate Petri dishes and housed in a screened field laboratory exposed to ambient forest conditions. Males were randomly assigned to a food diet (2 g sucrose per 200 ml distilled water) or

control diet (200 ml distilled water) soaked into cotton pieces. Males were checked daily and their cotton pieces were replaced every 3 days. Males were considered dead if they failed to right themselves when placed on their backs. Because data were not normally distributed, non-parametric Mann–Whitney (MW) tests were used to test the prediction that food availability extended male lifespan relative to control (one-tailed tests). Although initial age was unknown, selection bias was controlled by randomly assigning males to treatments. Five individuals of each species were frozen, dried at 60°C, and weighed to the nearest 1 µg. Voucher specimens have been placed in the collection of M. Kaspari at the University of Oklahoma.

Results

Both male aggregating species died shortly after capture, and neither lived longer when provisioned with food. All males of *Azteca* sp. died before feeding experiments could be established the day following capture (Table 1). Males of *A. colombica* lived at most 3 days regardless of the diet treatment (MW $U = 25.5$; $n = 7, 7$; $p = 0.47$; Fig. 1a). In contrast, males of both female calling species lived significantly longer when fed (Table 1). Food provisioned *E. ruidum* lived up to 33 days (MW $U = 2205.5$; $n = 45, 44$; $p < 0.03$; Fig. 1b) and *P. clavata* lived up to 116 days (MW $U = 62$; $n = 10, 10$; $p = 0.0006$; Fig. 1c).

Discussion

Whereas female ants may live for decades (Keller and Genoud, 1997), males appear specialized for a brief period of mate acquisition (Boomsma et al., 2005). Relative to females, males have diminished immune systems (Vainio et al., 2004; Baer et al., 2005), and chromosomes with shorter telomeres (Jemielity et al., 2007). Males also have reduced heads and mandibles, do not generate new sperm as adults (Hölldobler and Bartz, 1985; but see Heinze and Hölldobler, 1993), and lack metapleural glands (Brown,

Table 1 Summary data from male alate feedings experiments

| Subfamily | Taxon | Mating system | Collection date | N | Avg. mass of five males (±SD) | Avg. days alive (±SD) | | Range days alive | |
|----------------|---------------------------|---------------|---------------------|----|-------------------------------|-----------------------|---------|------------------|-------|
| | | | | | | Control | Food | Control | Food |
| Dolichoderinae | <i>Azteca</i> sp. | MA | 31 May | 80 | 0.58 ± 0.13 | <1 | <1 | NA | NA |
| Myrmicinae | <i>Atta colombica</i> | MA | 22 May | 14 | 48.04 ± 2.58 | 1 ± 1 | 2 ± 2 | 1–3 | 1–3 |
| Ectatomminae | <i>Ectatomma ruidum</i> | FC | 19 May and 7–9 June | 89 | 2.27 ± 0.20 | 7 ± 2 | 10 ± 7 | 1–12 | 1–33 |
| Paraponerinae | <i>Paraponera clavata</i> | FC | 3, 6 June | 20 | 26.44 ± 1.80 | 4 ± 3 | 36 ± 23 | 1–12 | 3–116 |

N total number of ants, Average mass is dry mass (mg). Mating syndromes indicated as follows: MA male aggregation, FC female calling. All collection dates in 2007

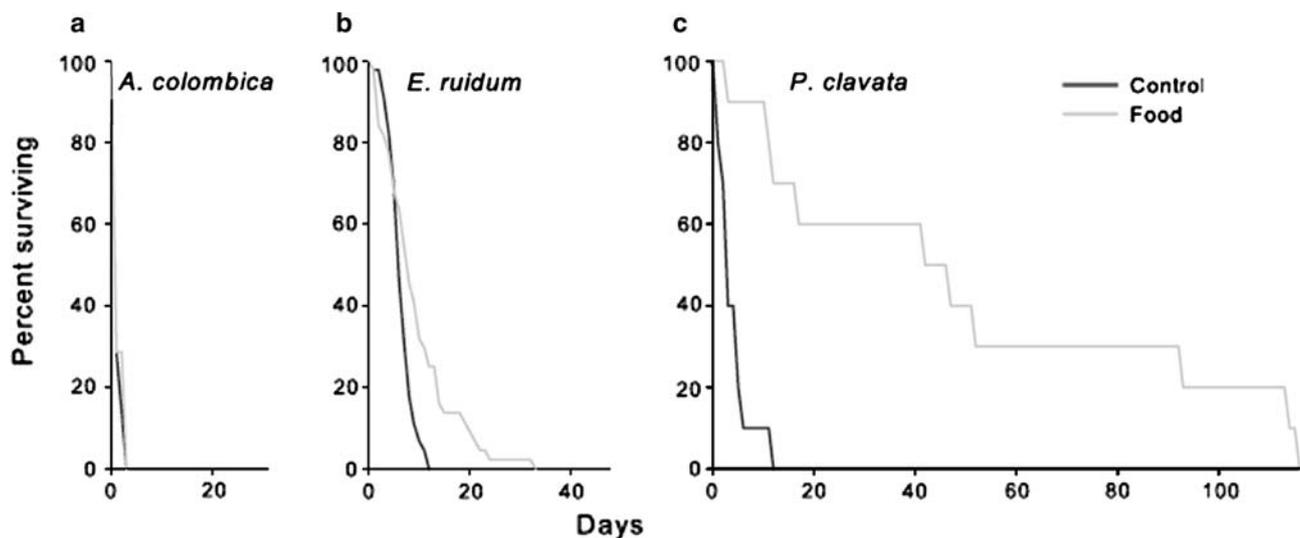


Fig. 1 Survivorship curves for males of *Atta colombica*, *Ectatomma ruidum*, and *Paraponera clavata* comparing control and food provisioned treatments

1968) that secrete antimicrobial compounds (Poulsen et al., 2002). Nevertheless, males of the ancestral, female calling syndrome, must survive long enough to find signalling females. Here, males of aggregating species invariably died soon after capture (Table 1; Fig. 1a), but males of calling species lived significantly longer when fed (Fig. 1b, c). Additionally, although larger taxa tend to live longer (Peters, 1983), males of *E. ruidum* far outlived males of *A. colombica* despite measuring less than 5% the body mass (Table 1). Combined, our results link male lifespan to mating systems and provide a framework to examine variation in costly traits such as capacities for immune response (Schmid-Hempel, 2005) and cellular maintenance (Keller and Jemielity, 2006).

These feeding experiments further suggest that males of calling species are free living, and underscore variation in male lifespan with important evolutionary implications. First, if males of calling species become increasingly costly to produce relative to female alates, mating systems may inform predictions about how a colony's investment in males translates into numerical sex ratios (Helms, 1994). Second, males that live longer and search for females may have greater mating frequency than ephemeral males of aggregating species (Bourke and Franks, 1995). Multiple mating appears common among longer-lived males of ancestral hymenopterans (Thornhill and Alcock, 1983; Boomsma et al., 2005). Third, the strength of sexual selection, often considered weak among social insects, is predicted to increase as male mating attempts become spread out over time (Emlen and Oring, 1977; Boomsma et al., 2005).

Although the present study suggests systematic variation in male lifespan, further comparative studies will be needed to test important assumptions. For instance, because

males in this study were captured in flight, longevity was estimated without the period before males left the natal colony. The lifespan of aggregating males may thus be underestimated if they must wait for nuptial flights that are synchronized across nests (Boomsma et al., 2005). In an extreme case, wingless males of the ant genus *Cardiocondyla* never disperse, and may live more than a year within the natal nest, defending harems of females (Yamauchi et al., 2006). In addition, female calling species are typified by small colony size, low population density, and social parasitism (Hölldobler and Bartz, 1985; Bourke and Franks, 1995; Mori et al., 2001). Linking these factors to variation in male traits should yield important ecological and evolutionary insights.

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References

- Baer B. 2003. Bumblebees as model organisms to study male sexual selection in social insects. *Behav. Ecol. Sociobiol.* **54**: 521–533
- Baer B., Krug A., Boomsma J.J. and Hughes W.O.H. 2005. Examination of the immune responses of males and workers of the leaf-cutting ant *Acromyrmex echinator*. *Insect. Soc.* **52**: 298–303
- Baer B. and Boomsma J.J. 2006. Mating biology of leaf-cutting ants *Atta colombica* and *A. cephalotes*. *J. Morphol.* **267**: 1165–1171
- Bartz S.H. 1982. On the evolution of male workers in the Hymenoptera. *Behav. Ecol. Sociobiol.* **11**: 223–228
- Boomsma J.J., Baer B. and Heinze J. 2005. The evolution of male traits in social insects. *Annu. Rev. Entomol.* **50**: 395–420

- Bourke A.F.G. and Franks N.R. 1995. *Social Evolution in Ants*. Princeton University Press, Princeton, New Jersey. 529 pp
- Brown W.L. 1968. An hypothesis concerning the function of metapleural glands in ants. *Am. Nat.* **102**: 188–191
- Cherif H., Tarry J.L., Ozanne S.E. and Hales C.N. 2003. Ageing and telomeres: a study into organ- and gender-specific telomere shortening. *Nucleic Acids Res.* **31**: 1576–1583
- Dobson F.S. and Oli M.K. 2007. Fast and slow life histories of mammals. *Ecosci.* **14**: 292–299
- Emlen S.T. and Oring L.W. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* **197**: 215–223
- Hahn D.A., Johnson R.A., Buck N.A. and Wheeler D.E. 2004. Storage protein content as a functional marker for colony-founding strategies: a comparative study within the harvester and genus *Pogonomyrmex*. *Physiol. Biochem. Zool.* **77**: 100–108
- Heinze J. and Hölldobler B. 1993. Fighting for a harem of queens: physiology of reproduction in *Cardiocondyla* male ants. *Proc. Natl Acad. Sci. USA* **90**: 8412–8414
- Heinze J. 2004. Reproductive conflict in insect societies. *Adv. Stud. Behav.* **34**: 1–57
- Helms K.R. 1994. Sexual size dimorphism and sex ratios in bees and wasps. *Am. Nat.* **143**: 418–434
- Hölldobler B. and Haskins C.P. 1977. Sexual calling behavior in primitive ants. *Science* **195**: 793–794
- Hölldobler B. and Bartz S.H. 1985. Sociobiology of reproduction in ants. In: *Experimental Behavioral Ecology and Sociobiology* (Hölldobler B. and Lindauer M., Eds), Sinauer Associates, Sunderland, Mass. pp 237–257
- Jemielity S., Kimura M., Parker K.M., Parker J.D., Cao X., Aviv A. and Keller L. 2007. Short telomeres in short-lived males: what are the molecular and evolutionary causes? *Aging Cell* **6**: 225–233
- Johnson R.A. 2002. Semi-claustral colony founding in the seed harvester ant *Pogonomyrmex californicus*: a comparative study of colony founding strategies. *Oecologia* **132**: 60–67
- Kaspari M., Pickering J., Longino J.T. and Windsor D. 2001. The phenology of a neotropical ant assemblage: evidence for continuous and overlapping reproduction. *Behav. Ecol. Sociobiol.* **50**: 382–390
- Keller L. and Passera L. 1989. Size and fat content of gynes in relation to the mode of colony founding in ants. *Oecologia* **80**: 236–240
- Keller L. and Genoud M. 1997. Extraordinary lifespans in ants: a test of evolutionary theories of ageing. *Nature* **389**: 255–263
- Keller L. and Jemielity S. 2006. Social insects as a model to study the molecular basis of ageing. *Exp. Gerontol.* **41**: 553–556
- Kozłowski J. and Weiner J. 1997. Interspecific allometries are by-products of body size optimization. *Am. Nat.* **149**: 352–380
- May R.C. 2007. Gender, immunity and the regulation of longevity. *BioEssays* **29**: 795–802
- Mercier J.L., Lenoir J.C., Eberhardt A., Frohschammer S., Williams C. and Heinze J. 2007. Hammering, mauling, and kissing: stereotyped courtship behavior in *Cardiocondyla* ants. *Insect. Soc.* **54**: 403–411
- Mori A., Grasso D.A., Visicchio R. and Le Moli F. 2001. Comparison of reproductive strategies in facultative and obligatory slave-making ants: the case of *Formica sanguinea* and *Polyergus rufescens*. *Insect. Soc.* **48**: 302–314
- Peters R.H. 1983. *The Ecological Implications of Body Size*. Cambridge University Press, Cambridge, Mass. 344 pp
- Poulsen M., Bot A.N.M., Nielsen M.G. and Boomsma J.J. 2002. Experimental evidence for the costs and hygienic significance of the antibiotic metapleural gland secretion in leaf-cutting ants. *Behav. Ecol. Sociobiol.* **52**: 151–157
- Reznick D.N. 1997. Life history evolution in guppies (*Poecilia reticulata*): Guppies as a model for studying the evolutionary biology of aging. *Exp. Gerontol.* **32**: 245–258
- Rolff J. 2002. Bateman's principle and immunity. *Proc. R. Soc. Lond. B* **269**: 867–872
- Schmid-Hempel P. 2005. Evolutionary ecology of insect immune defenses. *Annu. Rev. Entomol.* **50**: 529–551
- Sibly R.M. and Brown J.H. 2007. Effects of body size and lifestyle on evolution of mammal life histories. *Proc. Natl Acad. Sci. USA* **104**: 1–6
- Speakman J.R. 2005. Body size, energy metabolism and lifespan. *J. Exp. Biol.* **208**: 1717–1730
- Thornhill R. and Alcock J. 1983. *The Evolution of Insect Mating Systems*. Harvard University Press, Cambridge, Mass. 547 pp
- Trivers R.L. 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man, 1871–1971* (Campbell B., Ed), Aldine Press, Chicago, Ill. pp 136–179
- Tschinkel W.R. 1992. Brood raiding and the population dynamics of founding and incipient colonies of the fire ant, *Solenopsis invicta*. *Ecol. Entomol.* **17**: 179–188
- Vainio L., Hakkarainen H., Rantala M.J. and Sorvari J. 2004. Individual variation in immune function in the ant *Formica exsecta*; effects of the nest, body size and sex. *Evol. Ecol.* **18**: 75–84
- Vollrath F. and Parker G.A. 1992. Sexual dimorphism and distorted sex ratios in spiders. *Nature* **360**: 156–159
- Weber N.A. 1972. *Gardening in the Ants: the Attines*. American Philosophical Society, Philadelphia, Penn. 146 pp
- Wiernasz D.C., Sater A.K., Abell A.J. and Cole B.J. 2001. Male size, sperm transfer, and colony fitness in the western harvester ant, *Pogonomyrmex occidentalis*. *Evolution* **55**: 324–329
- Yamauchi K., Ishida Y., Hashim R. and Heinze J. 2006. Queen-queen competition by precocious male production in multiqueen ant colonies. *Curr. Biol.* **16**: 2424–2427
- Zuk M. and McKean K.A. 1996. Sex differences in parasite infections: patterns and processes. *Int. J. Parasitol.* **26**: 1009–1024